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Spatial Patterns of Winter Roadside Gray Wolf Sightability in Yellowstone National Park

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Spatial Patterns of Winter Roadside Gray Wolf Sightability in Yellowstone National Park

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ABSTRACT

Imperfect detection is ubiquitous among wildlife research and can affect research conclusions and management. Detection probability is often included in observation-based models. We leveraged research of gray wolves *(Canis lupus)* in northern Yellowstone National Park (YNP) to evaluate how the probability of sighting radio collared wolf packs from ground-based observation locations was affected by the characteristics of each spatial location (i.e., distance from the road, visibility (from a viewshed analysis), habitat openness, carcass presence, and wolf group size). We used two complementary approaches focusing on sightings during early (mid-November to mid-December) and late (March) winter periods between 1995 and 2017. First, we used 2,681 unique, daily observations of 17 wolf packs collected during 44 unique 30-day winter monitoring periods. We then compared these ground observations to the same number of random locations, each sampled from within wolf pack home ranges. Using this dataset, we used conditional logistic regression to estimate the probability of observing a group of wolves. Second, we used information on continuous observations of wolves collared with Global Positioning System (GPS) radio collars. We developed a similar probability of observing a group of wolves using logistic regression, but we compared GPS locations where wolves were observed from the ground crews to location where wolves were known to not be observed. We termed the first analysis a used-available model, and the second a used-unused model in accordance with the field of resource selection functions. Using the used-available model, we found that the probability of wolf sightings declined as wolves were farther from the road and increased when wolves were in open, visible areas and when wolves were in larger groups. These results were very similar to the used-unused model developed with only GPS-collared wolf locations. The top model included the same covariates, which each had the same directional effect on the probability of seeing wolves. We used our results to build spatial predictions for seeing wolves in YNP. These predictions are useful to managers for identifying "hot-spots" of wolf observations and can be incorporated into research related to wolf ecology and predator-prey dynamics that relies on observations of wolves.

ACKNOWLEDGEMENTS

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INTRODUCTION

Imperfect wildlife detection is a fundamental challenge to a variety of aspects of wildlife biology and management, including population estimation and behavioral studies (Buckland et al. 2001). The consequences of imperfect detection are often underestimated because they are ignored. In general, the problem of imperfect detection permeates all wildlife studies, but is particularly severe for rare and elusive species. For example, marine mammals spend all or most of their time underwater, and the detection of some species, such as whales, during surveys to estimate population abundance is impacted by proximity to the surface of the ocean, the only time they are available to be visible during aerial surveys (Hain et al. 1999, Buckland et al. 2001). In addition, the common practice of helicopter surveys to estimate ungulate abundance for harvest management, such as for moose *(Alces alces)*, are impacted by moose behavior, forest cover, and proximity to the helicopter (Buckland et al. 2001, Peters et al. 2014).

Many methods have been developed to address the problem of imperfect detection and, accordingly, estimate the number of individuals missed during surveys (Buckland et al. 2001). An example is the missed proportion of the population on aerial surveys. Another is sightability modeling, which attempts to estimate the probability of observing the species of interest and eliminate bias in population counts (Fieberg, 2012). For example, elk *(Cervus elaphus)* sightability models which were developed by estimating the probability of sighting known radio collared individuals in Montana, and then validated in Idaho indicated that on average only 60-90% of elk were observed on helicopter surveys (Samuel et al. 1987, Unsworth et al. 1990, Samuel et al. 1992). Sightability is also an important component in mark-recapture studies, which consist of capturing individuals, marking them, releasing them, and capturing them again to estimate detection probability, and thus, estimate population size (White, 2005). Distance sampling is another method of estimating population size in which density is calculated by measuring the distance from a transect or line to the animal, an example is point counts on birds (Buckland et al. 2001, White, 2005). Common among these surveys is that distance negatively affects detection, but this is also altered by factors such as habitat characteristics and species type. The cost of imperfect detection in wildlife biology can be significant, leading most often to underestimating abundance which can affect management and conservation decisions.

Large carnivores are known for their elusive nature and are among the most difficult animals to observe in the wild. This makes it difficult to study their ecology and makes data harder to obtain, causing management and conservation decisions to be made with less knowledge, which are especially important because of the worldwide global declines in their populations (Ripple et al. 2014). Large carnivores occur at lower densities than prey species, and secretive behavior causes them to be difficult to detect. This is often due to habitat loss and the negative effects of human activity such as hunting and persecution. Some examples include snow leopards *(Panthera uncia)* in Asia, which live in remote areas and are difficult to see due to their coloration, mountain lions *(Puma concolor)* in Northern America, which are secretive and difficult to view, and brown bears *(Ursus arctos)* in Europe, which are persecuted and avoid humans. Gray wolves *(Canis lupus)* are also well known for their elusive nature, in addition to their ability to avoid detection because of a long history of persecution by humans (Musiani and Paquet 2004, Mech et al. 2010).

Large carnivore ecology and management is impacted by studies of predator-prey dynamics, and yet often do not address issues of imperfect detection. Both behavioral studies and studies of predator-prey dynamics of large carnivores can be affected by detection issues. For example, wolf research in Yellowstone National Park (YNP) has benefited by the visibility of the study subjects, which has enabled new insights into wolf behavior and predator-prey dynamics previously unknown because their tendencies to avoid people cause them to live in remote areas (Smith et al. 2004, Cassidy et al. 2015). Another example of highly visible carnivores is the observation of wild African lions *(Panthera leo)* in the Serengeti National Park in Tanzania, Africa. (Packer et al. 2005).

In addition to behavioral observations, a fundamental reason why many large carnivores are studied is to estimate the effect of predators on prey populations. In doing so, ecologists often estimate kill rate, a statistic which describes the number of prey killed per predator per unit time (Mills, 2012). Studies of kill rates can reveal how the number of prey killed changes with predator density, which describes one of the foundational concepts in ecology, the functional response of a predator (Holling, 1959). Biologists use several methods to estimate kill rates including aerial location of carcasses (Ballard et al. 2001), snow tracking (Hebblewhite et al. 2002), and searching clusters of Global Positioning System (GPS) data (Anderson et al. 2003, Sand et al. 2005, Webb et al. 2008). These methods usually assume perfect detection, which is unlikely to be a reasonable assumption for most studies.

However, in more open settings, for other carnivores, biologists estimated kill rates using visual observations. These observations may either be aerial or ground-based (Ballard et al. 2001). For example, ground-based observations were used to study African lions in the Serengeti (Packer at al. 2005). Ground observation led to determining the dynamics of lion prides, including lion kill rates via detecting kills, based on ecological factors. African wild dogs *(Lycaon pictus)* were also studied using ground observations of their hunting behavior (Estes and Goddard, 1967). Smith et al. (2004) also developed a “double-count” method to estimate the probability of detecting a kill, and hence, wolf kill rate based on independent monitoring by aerial and ground-based observations in Yellowstone. Very few other researchers, however, have estimated detection probability of carnivore kill rates.

Wildlife tourism in many national parks and elsewhere is also driven by wildlife sightings (Boyle and Sampson, 1985). However, wildlife distributions are also conversely affected by tourism, often leading to sensitive species, such as carnivores, avoiding areas of high tourism, requiring management to reduce negative impacts of too much tourism (Rogala et al. 2011, Borg et al. 2016). For example, visits from tourists seeking to view brown bears in McNeil River Sanctuary are limited to ten visitors a day in the summer to reduce stress to bears (Aumiller and Matt, 1984). Similarly, there are instances of tigers *(Panthera tigris)* in India becoming habituated to people, which can lead to negative effects on tiger survival (Sharma et al. 2010). Polar bears *(Ursus martimus)* in Churchill also are impacted by tourism, displaying agitated behavior when they are being observed by people (Dyck and Baydack, 2004). In YNP, gray wolves are commonly viewed by visitors, and both behavioral interactions and wolf kill rates are influenced by the park road and visitors (Kauffman, 2007). Wolf visibility has also been important for growth in tourism (Duffield et al. 2008), and recent studies estimate that more people are likely observe wolves in Yellowstone than any other setting in the world, up to 50,000 per year (Smith, 2013). Therefore, wildlife observation can have both positive and negative effects, and this includes gray wolves in Yellowstone. Despite the importance of roadside sightings to both Yellowstone park research and management, the ecology of wolf sightings from a road has not been thoroughly researched.

Here, we evaluated what factors affected the likelihood of successful ground-based observations of wolves in northern YNP and the immediate surrounding area. To do so, we used data obtained during two annual 30-day winter observation periods from 1995 – 2017 (Smith et al. 2004). We estimated factors affecting wolf sightability in two complementary ways based on the field of resource selection functions (RSF, Manly et al. 2002). Firstly, we compared wolf observations to random points located within the pack's home range using a used-available RSF design. Secondly, we used wolf GPS locations and compared the locations when wolves were in or out of sight using a used-unused RSF design.

We tested five major hypotheses of factors affecting wolf sightability. We first predicted that wolves would be easier to see close to the road following decades of studies (Buckland et al. 2001, Smith et al. 2004). We also predicted detection probabilities would be higher in areas that were physically visible from the road, which is akin to the availability constant of whales being unavailable to be observed when not near the surface of the ocean (Buckland et al. 2001). Thirdly, we hypothesized that wolves would be more visible in areas of more open canopy cover, in addition to whether an area was physically visible from the road. We then hypothesized that wolves would be easier to observe in larger group sizes (i.e., larger packs would be easier to see), based on the well-known positive effect of group size on detection of many species (Unsworth et al. 1990). We also predicted that wolves on carcasses would have higher probabilities of detection (due to continued presence and scavenger presence), as posited by Smith et al. (2004) because of the effect of raven *(Corvus cortax)* and other scavenger activity. Finally, we made spatial maps of the predicted probability of observing wolves from the road to provide a useful tool for park managers.

METHODS

Study Area – Our study area was defined by the movements of 17 wolf packs over 44 winter study periods (3.6 pack years) that were monitored by ground observation crews within the Northern Range of Yellowstone National Park and surrounding national forests (Figure 1). Winters, when we conducted our study, tend to be long and cold, with snow generally covering the ground throughout (Houston 1982). Elevations range from 1500-2400 meters (Houston 1982). Vegetation in the study area ranges from lower elevation montane ecoregion Douglas firs *(Pseudotsuga Menziesii)*, Wyoming big sage-brush *(Artemisia tridentae)*, and grasslands dominated by *Festuca sp.* to more closed canopied lodgepole pine *(Pinus contorta)*, subalpine fir *(Abies lasiocarpa)*, and eventually whitebark pine *(Pinus albicaulis)* at higher elevations in subalpine regions. The study area also contains abundant wildlife, including ungulates such as American bison *(Bison bison)*, American elk *(Cervus elaphus)*, and mule deer *(Odocoileus hemionus)*, and large carnivores, such as grizzly bears *(Ursus arctos)*, black bears *(Ursus americanus)*, and cougars *(Puma concolor)*. The study area is transected by the park road, which provides access for tourists and researchers and serves as the main platform for observing wolves. The portion of the study area inside YNP is protected from human disturbance, with no disturbance of wildlife allowed in the park, however, some wolves were able to be legally trapped or hunted outside YNP beginning in 2009.

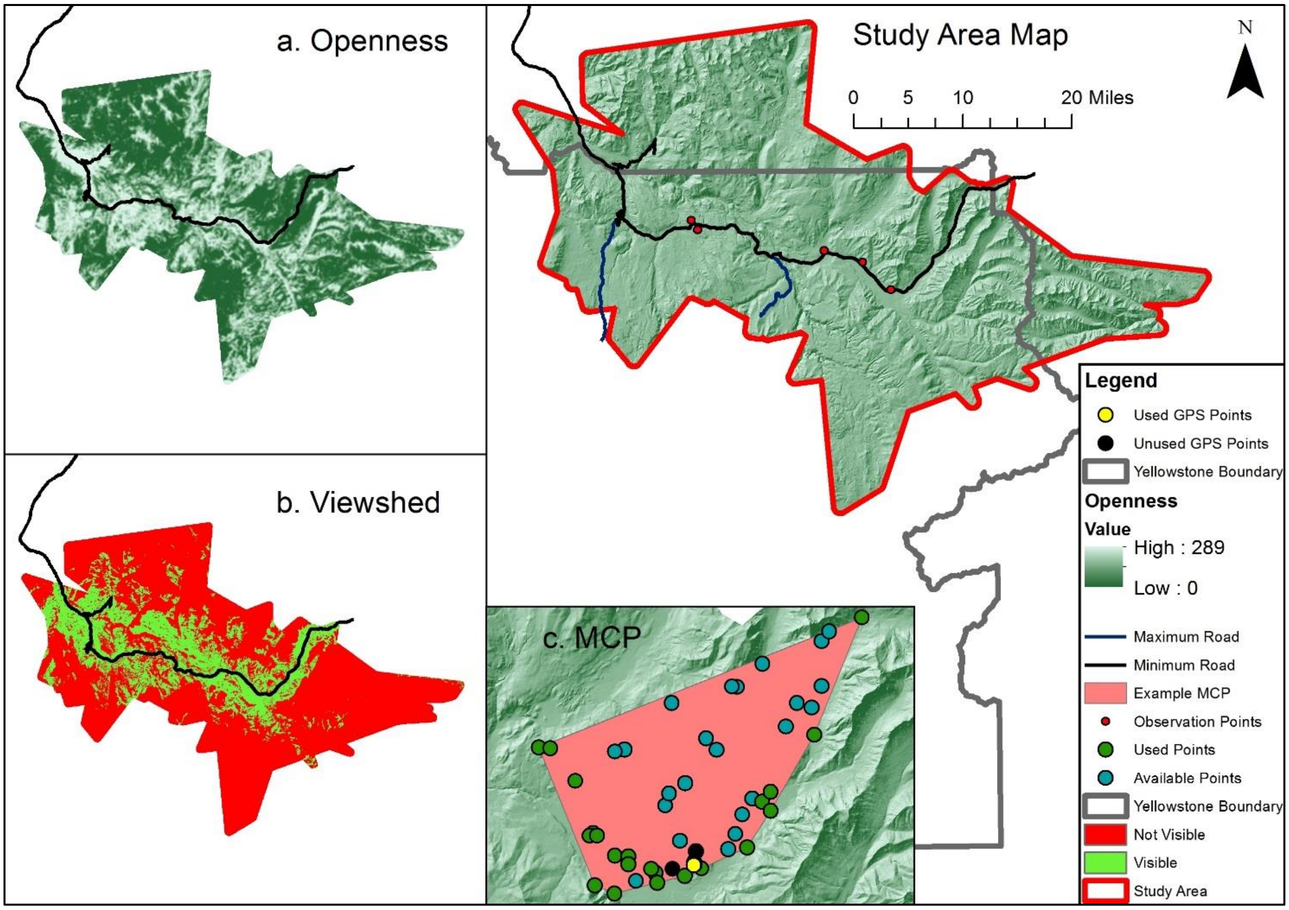

Figure 1 – Map of study area extending to maximum spatial extent of gray wolf *(Canis lupus)* packs in the Northern Range of Yellowstone National Park in winter. The minimum road is the only road open all year. The maximum road was used occasionally to observe wolves (4 out of 130 pack study periods). Points used by wolves and available points are shown. Inset figures show a) a continuous openness layer (Kohl et al. 2018), b) a viewshed from the park road and key observation points (red dots in main panel) created in ArcGIS 10.4, and c) an example minimum convex polygon (MCP) was created from data from the Lamar Canyon pack in March 2012 showing example wolf sightings (used) and random available locations generated within the MCP. In addition, used and unused GPS points from 832F from 7 March 2012 are shown.

Winter Study – Winter study observations began in early winter 1995 (Smith et al. 1999). We placed collars on wolves during the winter using helicopter capture through net gunning or aerial darting. Both GPS and VHF collars were deployed. Wolf capture and handling conformed to the National Park Service (NPS) animal capture and handling policies, as well as the University of Montana IACUC protocol AUP 043-15 to M. Hebblewhite.

We collected data on wolf sightings during two annual 30-day winter study periods, the main goal of which is the long-term study of wolf prey and wolf ecology in YNP (Smith et al. 2004). Within each year, the first period took place in early winter (generally 15 November – 14 December) and the second in late winter (generally 1 March – 30 March). During these periods, one ground observation crew of 2 – 3 people was assigned to 2 or usually 3 radio-collared wolf packs (Table 1). These ground-based observation crews attempted to locate the wolf pack using radio telemetry, and then observe their behavior during all daylight hours (Smith et al. 2004). As such, ground observation crews attempted to observe wolf packs throughout each day.

We used these observation data of wolf sightings in two ways. First, for all packs that were monitored by ground -based observation crews, we recorded the first location where wolves were observed each day and paired that data with random locations in a used-available sightability model framework (Figure 1c, see *Study Design* below for details). Then, for a subset of these packs that contained GPS collared individuals, we used the observation data ground observation crews gathered throughout each day and determined whether the wolf was in sight by the crews during each time the GPS collar recorded a location. This data was used in a used-unused framework (Figure 1c, see *Study Design* below for details).

Table 1 – Total number of observations and GPS data by pack collected to create a sightability model of gray wolves *(Canis lupus)* in Yellowstone National Park in winter. We collected observations during two annual winter study periods beginning in late winter 1995 and concluding in early winter 2017.

Pack	**Observations**	**GPS Locations**
Eightmile (5)	90	1210
Agate Creek (5)	82	1093
Blacktail Plateau (11)	234	1933
Crystal Creek (2)	13	0
Druid Peak (23)	526	175
Mount Everts (1)	25	356
Geode Creek (6)	126	414
Hellroaring Creek (3)	52	0
Junction Butte (8)	161	2039
Lamar Canyon (13)	253	1167
Leopold (25)	545	1146
Oxbow Creek (2)	56	343
Prospect Peak (5)	115	1659
Quadrant Mountain (2)	34	0
Rose Creek (14)	233	0
Silver (1)	24	0
Slough Creek (4)	112	334
Total (130)	**2681**	**11869**

Used-available Analysis – We developed our first statistical model of wolf viewability using a used-available RSF framework (Manly et al. 2002), comparing the wolf sighting locations to random locations created in Program R (R Core Team, version 3.4.1, 2017). Ground crews recorded the spatial location on a topographic map, group size, and whether a carcass was present for every sighting. We used wolf sightings from the two to three packs observed in each winter study period as the dependent variable in binomial models to understand what factors affected the probability of sighting wolves.

For the used-available model, we first created minimum convex polygons (MCPs) using wolf collected through either aerial or ground-based observations (Figure 1c). Specifically, for each day, we developed our MCPs using one randomly selected aerial or ground observation. If a pack was in multiple 'groups' (i.e., wolf packs are not always together) and we had observations for more than one group, we developed the MCP using randomly selected locations for each group. Upon developing a MCP for each pack, we then created random points for our used-available analysis in a 1:1 ratio with wolf sightings (n = 2,681 total locations) within each pack's territory.

Sightability Covariates - We created viewshed layers of the combined area of the MCPs from the park road and key wolf observation points using ArcGIS 10.4 (Figure 1b). We created two viewsheds, one using the main park road open in winter which extends beyond the park, and an additional one using extensions of the road that are closed to the public but are sometimes used during winter study for certain packs. Spatial covariates were estimated specific to the road used for a pack during that winter study. The viewshed represents what is available to be viewed. We used a continuous openness layer of the park in which the value of each pixel is described by the openness of adjacent pixels (Kohl et al. 2018) (Figure 1a, Figure 2b, Figure 3b). We also measured the distance of each point to the road in Program R (R Core Team, version 3.4.1, 2017). Additionally, we used group size and the presence of a kill as covariates, because previous studies often show animal group size is positively related to sightability (Samuel et al. 1987, Unsworth et al. 1990, Samuel et al. 1992) and because we reasoned that the presence of a kill-site might make wolves more visible because of raven activity (Smith et al. 2004).

Sightability Model - We then estimated wolf sightability using conditional logistic regression (also called matched-case control logistic regression) models where each used location was paired with a random available location (Compton et al. 2002, Whittington et al. 2005). The conditional logistic regression model is described by the equation P(Sightability) =

logit(β_1 Viewshed + β_2 Distance + β_3 Openness + β_4 Carcass + β_5 Group Size + β_6 Group Size * Covariate + ε_{ik}). Equation 1 where β_1 is the coefficient for the effects of viewshed on the probability of sighting a wolf, β_2 is the coefficient for the effects of distance from the park road on the probability of sighting a wolf, β_3 is the coefficient for the effects of habitat openness on the probability of sighting a wolf, β_4 is the coefficient for the effects of carcass presence on the probability of sighting a wolf, β_5 is the coefficient for the effects of group size on sighting a wolf, β_6 is the effect of the interaction between group size and either distance or openness on sighting a wolf, and ε_{ik} is the variance. For group size, we assigned each random available location group size as the same as its paired sighting. Because group sizes were thus similar, we could only test for the effect of group size on the probability of observing a wolf in interaction with other continuous covariates, similar to Fortin et al. (2009) and Berger et al. (2015). Of note, because of the arbitrary sampling of availability, the true probability of observing wolves is unknown in a used-available design, so there is no intercept value (i.e., no β_0, see Manly et al. 2002, Compton et al. 2002). We conditioned the variance (ε_{ik}) on each pair of used-available locations as the strata (k=1…n paired used-available locations) for conditional logistic regression.

Used-unused Analysis - Secondly, we developed a complementary sightability model using wolf GPS data in a used-unused (or observed/unobserved design). We first determined whether a GPS-collared wolf in a pack was observed by comparing daily observations from the ground observation crews to each GPS location. We did this by manually determining whether each GPS point was in sight or out of sight based on daily observation forms recorded by ground observation crews. We also determined the group size for each point and whether the wolves were on a carcass (an example of how we linked GPS location data to field observations are given in Appendix 3 - 5). Generally, GPS collars recorded points every hour, but there were some exceptions in which locations were recorded at different fix intervals (e.g., daily). We compared GPS locations where wolves were observed to locations where wolves were not observed, akin to a true used-unused RSF design (Manly et al. 2002) as follows P(Sightability) = logit(β_{0i} + β_{1i} Viewshed + β_{2i} Distance + β_{3i} Openness + β_{4i} Group Size + ε_i). Equation 2 where β_1 is the coefficient for the effects of viewshed on the probability of sighting each wolf location I = 1…n, β_2 is the coefficient for the effects of distance from the park road on the probability of sighting a wolf, β_3 is the coefficient for the effects of habitat openness on the probability of sighting a wolf, β_4 is the coefficient for the effects of group size on sighting a wolf, e is the error, and β_0 is the baseline probability of observing a GPS collared wolf independent of covariates because of the true used-unused, observed-unobserved design (Manly et al. 2002).

We limited the GPS data to daylight observations (i.e., those locations that occurred between 8:00 and 17:00). We used data from 12 different packs and 31 different collared wolves. We only included wolves if they were usually with other members of their pack. Some packs contained multiple GPS collars, therefore we initially selected the individual that was most representative of their pack's movements. We did so because ground-based observation crews were focused on the 'pack'. If multiple wolves were core members of the pack, we first selected the wolf if its collar had an hourly schedule. We also considered if the wolf did not survive the study period. If both individuals met the above criteria, we randomly selected a wolf and removed the remaining individual. For each GPS location, we classified the wolf as being in sight, out of sight, or unknown (e.g., not available, NA, see appendices 3-5). We also determined the size of the group at each observed GPS location. In addition, we incorporated the same covariates as for the used-available design above, including both measures of distance (e.g., to the road), openness, and group size (Figure 2b). We did not use the carcass presence variable in this analysis due to its unimportance in the used-available analysis (see results) and the uncertainty of the presence of wolves on a carcass when they were not in view.

Statistical Analysis – All analyses were conducted in version 3.4.1 of Program R (R Core Team 2017). We estimated conditional logistic regression models for the used-available analysis in equation 1 using the package `survival` (Therneau and Grambsch, 2000). We estimated the used-unused and used-available sightability models using generalized linear models (GLM) with the logistic link function in the package `lme4` (Bates et al. 2015) and considered a random effect for each wolf pack for the used-unused analysis in equation 2 (Gillies et al. 2016). For both analyses, we used scaled covariates when we used continuous covariates to facilitate evaluation of effect size and comparison between models. We created a-priori candidate model sets that were similar between both sightability models based on the hypothesized importance of our covariates and key ecological interactions. We created all combinations of additive models using the viewshed, openness, distance to road, group size, and carcass presence covariates and created strategic interaction models. These interaction models included distance and carcass presence, distance and group size, openness and carcass presence, and openness and group size. Then, we evaluated the top models using Akaike Information Criterion (AIC) and used variable importance weights as an indicator of the relative contribution of each of our covariates to wolf sightability (AIC, Burnham and Anderson 1998). Finally, we evaluated the performance of the top used-unused model using standard logistic regression diagnostics, and report the overall classification success, the confusion matrix of classification of observed and unobserved wolf locations, sensitivity (probability of correctly classifying observed locations), specificity (probability of correctly classifiying unobserved locations), and the Area Under the Curve (AUC) (Hosmer and Lemeshow, 2000) that measures overall model performance.

RESULTS

Over the study periods, 2,681 observations of wolf groups were made from ground observations, which were paired with an equal number of available locations within MCPs In addition, 3,001 GPS locations were classified as observed (used) and a remaining 8,868 were not observed (unused). The slight difference in the GPS points is due to wolves being in sight (used) or out of sight (unused) as opposed to the used-available analysis, in which we created an equal number of random points to observations. For the used-available data, the average distance of an observation from the road was 2,601 ± a standard error of 30.71 meters (Figure 2a). The average distance of used GPS points from the road was approximately 2,414 ± 22.19 meters compared to 3,477 ± 28.57 meters for unused points (Figure 3a). The average size of a wolf group was approximately 9 ± 0.06 individuals for the used-available data. The average size of a wolf group was approximately 10 ± 0.07 individuals for used GPS points.

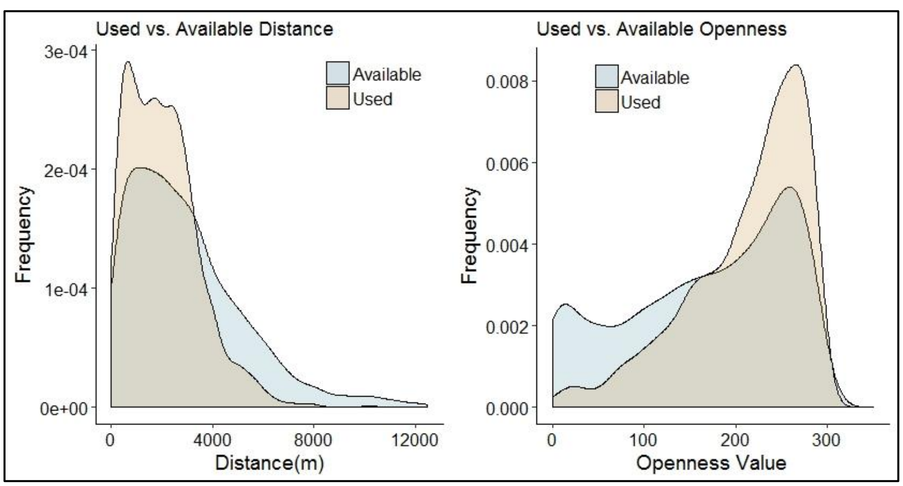

Figure 2 – Histograms of distance to the park road in meters (a) left) and openness (b) right) for each gray wolf *(Canis lupus)* observation used to create sightability models in Yellowstone National Park and surrounding areas using a used-available analysis. Openness runs on a scale from low (0) to high (289).

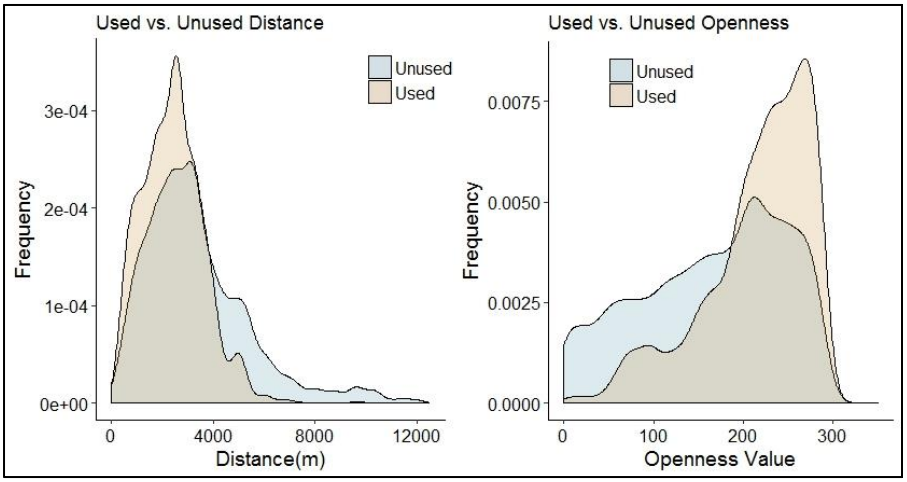

Figure 3 – Histograms of distance to the park road in meters (a) left) and openness (b) right) for each gray wolf *(Canis lupus)* observation used to create sightability models in Yellowstone National Park and surrounding areas using a used-unused analysis. Openness runs on a scale from low (0) to high (289).

Used-Available Analysis – The top wolf sightability model in the used-available analysis included an interaction between openness and group size, whether the location was visible in our viewshed, and distance to the park road (Table 2, Appendix 1). This model contained 49% of the AIC weight across the top model set. Of the top 5 models, all included viewshed value, openness value, and distance to the road as covariates. Group size was in the top model, and held 62% of the AIC weight, suggesting group size was important, but not as important as the other three core variables (Table 2). However, this lesser value may be due to equal group sizes between paired used and available points. Carcass presence only held 10% of the total AIC weight (Table 2).

Table 2 – Top models of roadside winter gray wolf sightability in Yellowstone National Park. These models were created using a used-available analysis. Data was collected during two annual winter study periods from 1995-2017.

Model	LL	K	Delta AICc	AICcWt	Cum.Wt
Openness * Group Size + Viewshed + Distance	-1517.33	5	0.00	0.49	0.49
Viewshed + Distance + Openness	-1519.92	3	1.16	0.28	0.77
Distance * Group Size + Viewshed + Openness	-1518.68	5	2.70	0.13	0.90
Distance * Carcass + Viewshed + Openness	-1519.36	5	4.06	0.06	0.96
Openness * Carcass + Viewshed + Distance	-1519.91	5	5.16	0.04	1.00

Overall, the beta coefficients from the top model indicated that the probability of detecting a wolf was higher in more visible areas from the road (Table 3, Figure 4, $\beta = 0.34$, SE = 0.072). In addition, wolves were more likely to be detected in areas with higher openness values (Table 3, Figure 5, $\beta = 0.53$, SE = 0.037). Finally, the probability of detecting a wolf from the road decreased by approximately 42 % for every 100 m the wolf was from the road (Table 3, Figure 4-6, $\beta = -0.53$, SE = 0.045). All p-values were less than 0.05, indicating statistical significance for covariates in our top model. As mentioned in the methods, the group size coefficient, however, was not estimable due to the use of conditional logistic regression models because it was fixed for both used and available locations. However, the interaction indicates that the probability of detecting a group of wolves in areas with low openness values was smaller when the group size is smaller (Table 3, β = 0.085, SE = 0.038). In addition, we created used-available probability maps for a pack of 4 wolves, a pack of 12 wolves, and the difference between the two groups.

Table 3 – Conditional logistic regression beta coefficients (Coef, β) from the top used-available analysis model regarding winter roadside gray wolf sightability in Yellowstone National Park. We gathered data during winter study periods between 1995 and 2017. The model is Openness * Group Size + Viewshed + Distance. This model contained 49% of the cumulative AIC value. Also shown are the scaled odds ratio (Exp Coef), SE, Z-value, and P -value.

	Coef (β)	Exp(Coef)(Scaled)	SE(Coef)	Z	Pr(>|z|)
Viewshed (0,1 category)	0.34	1.408e+00	0.072	4.756	1.98e-06
Distance	-0.53	9.998e-01	0.045	-11.744	< 2e-16
Openness	0.53	1.005e+00	0.037	14.418	< 2e-16
Group Size	NA	NA	0.000	NA	NA
Openness:Group Size	0.08	1.000e+00	0.038	2.235	0.0254

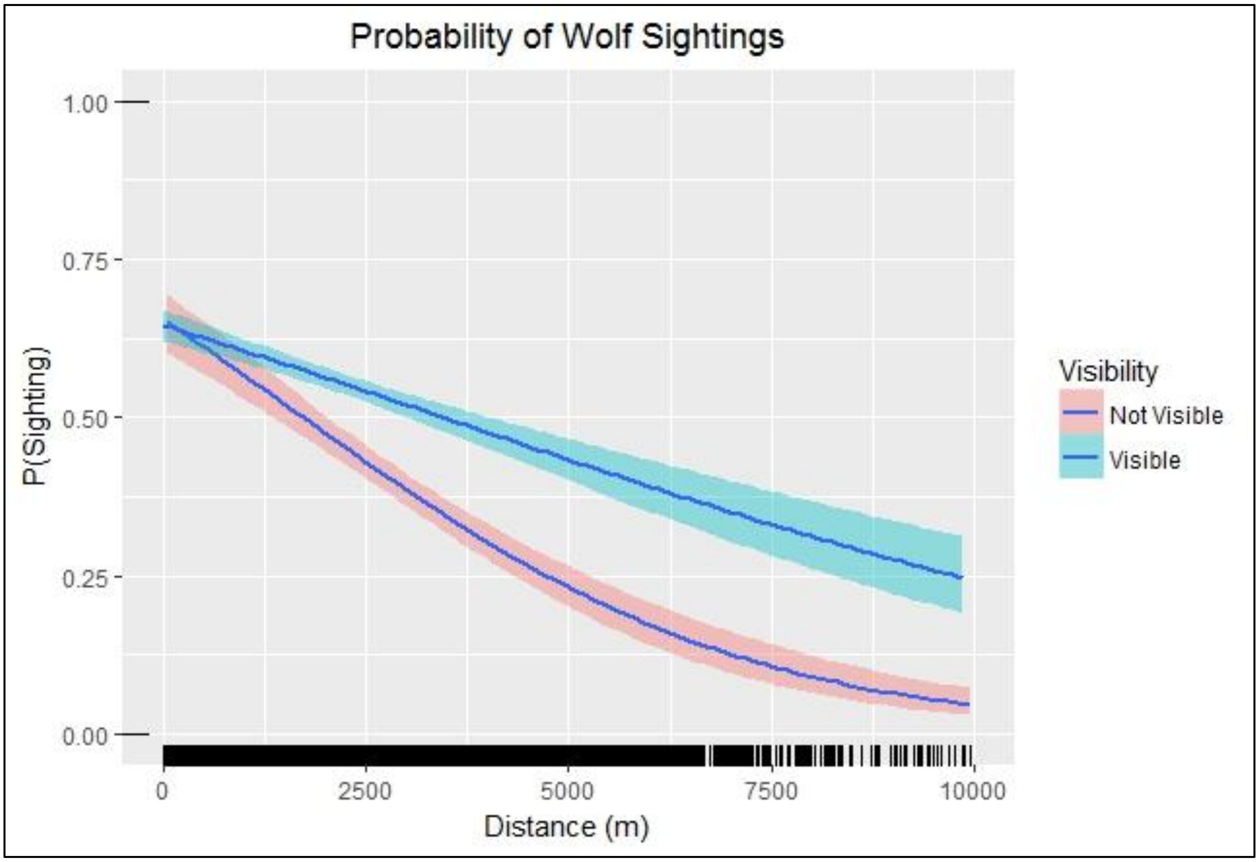

Figure 4 – Predicted probability plot of the relationship between distance to the road in meters (X) and the probability of detecting a gray wolf *(Canis lupus)* in Yellowstone National Park from 1995-2017in areas that are visible and not visible from the road in the used-available analysis. Although both categories have a similar probability near the road, the probability drops off dramatically as distance from the road increases. Overall, visible areas have a higher likelihood of wolf observations.

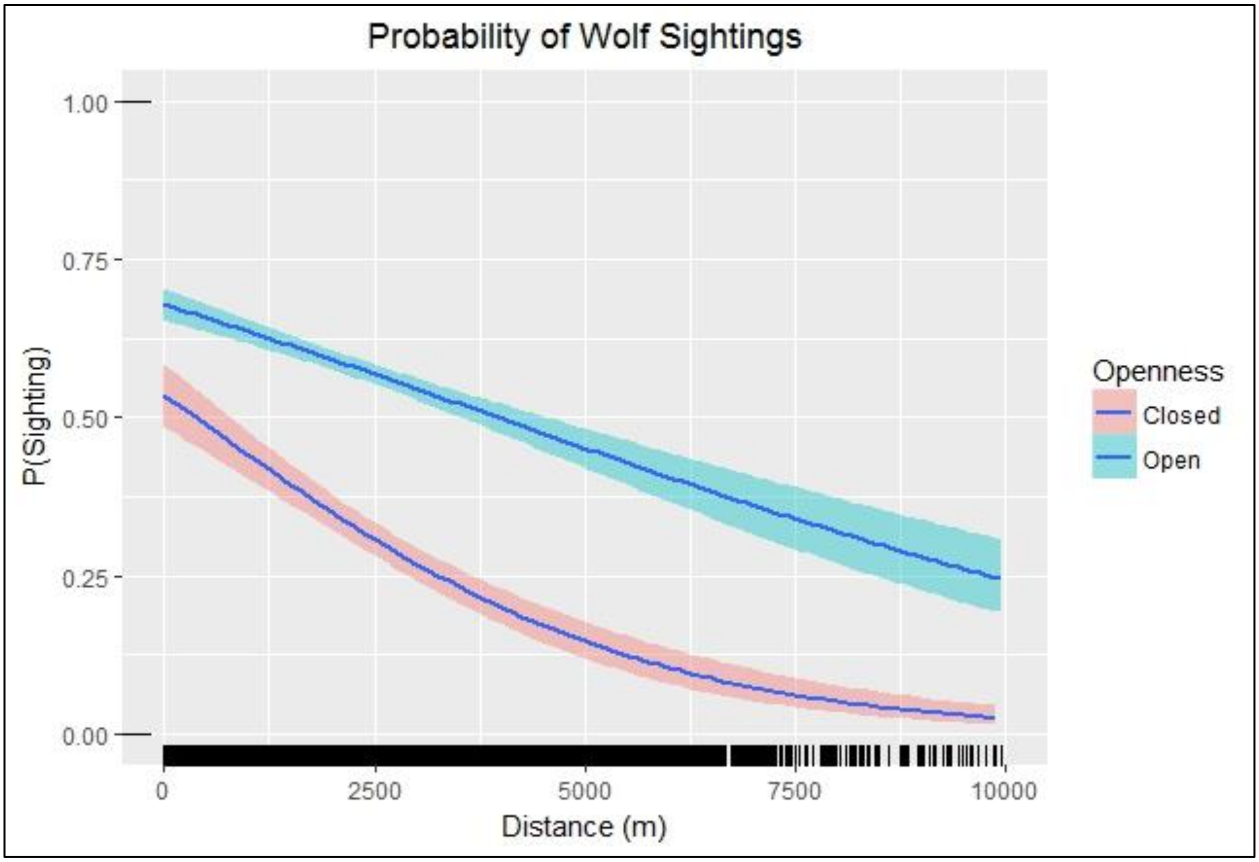

Figure 5 – Predicted probability plot of the relationship between distance to the road in meters (X) and the probability of detecting a gray wolf *(Canis lupus)* in Yellowstone National Park from 1995-2017 in areas that are open and closed in the used-available analysis. For this graph, the continuous openness category was split down the middle to create two categories. In both categories the probability of detecting a wolf drops off dramatically as distance from the road increases. Overall, open areas have a higher likelihood of wolf observations.

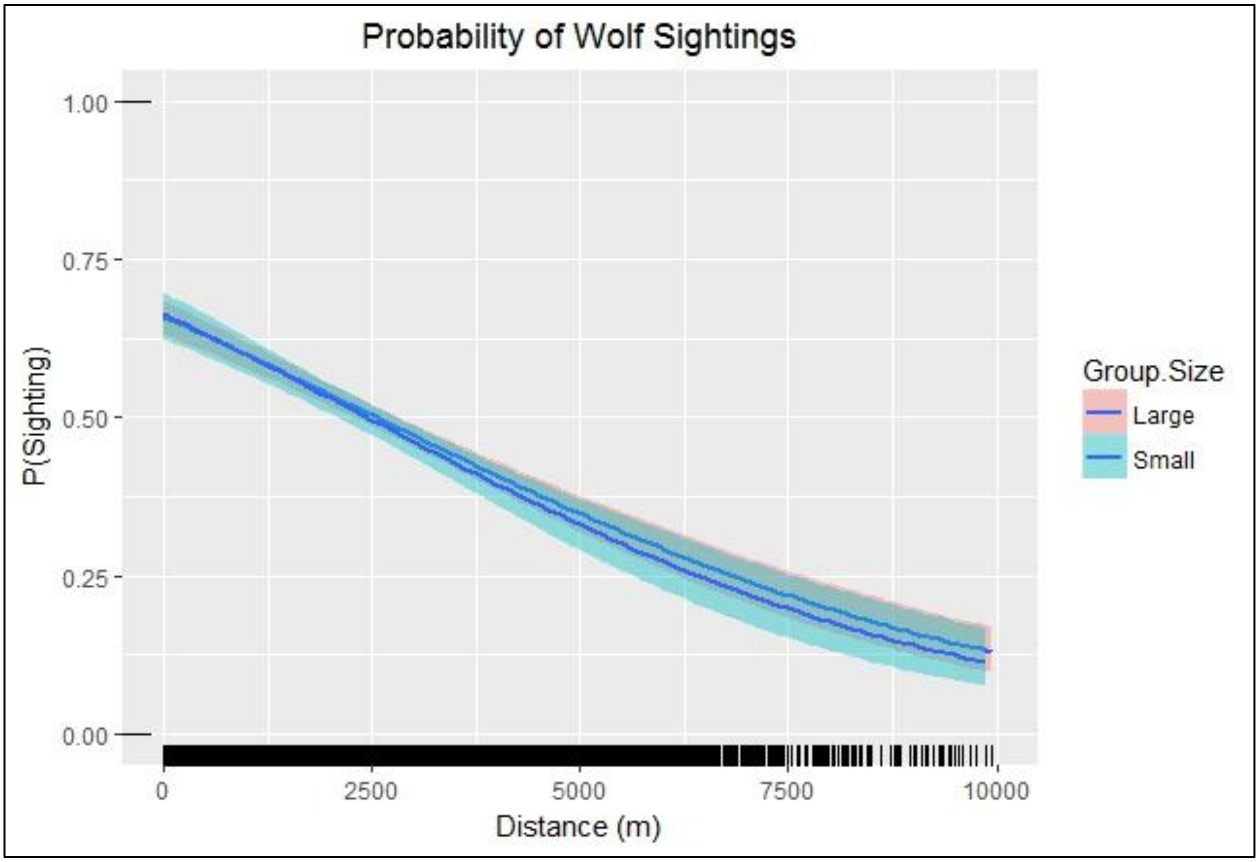

Figure 6 – Predicted probability plot of the relationship between distance to the road in meters (X) and the probability of detecting a gray wolf *(Canis lupus)* in Yellowstone National Park from 1995-2017 in large and small groups in the used-available analysis. For this graph, groups consisting of 8 or more wolves were considered large groups, while groups consisting of 7 or less were considered small groups. In both categories the probability of detecting a wolf drops off dramatically as distance from the road increases. Overall, larger groups have a slightly higher probability of detection, especially at distance, although the difference is small.

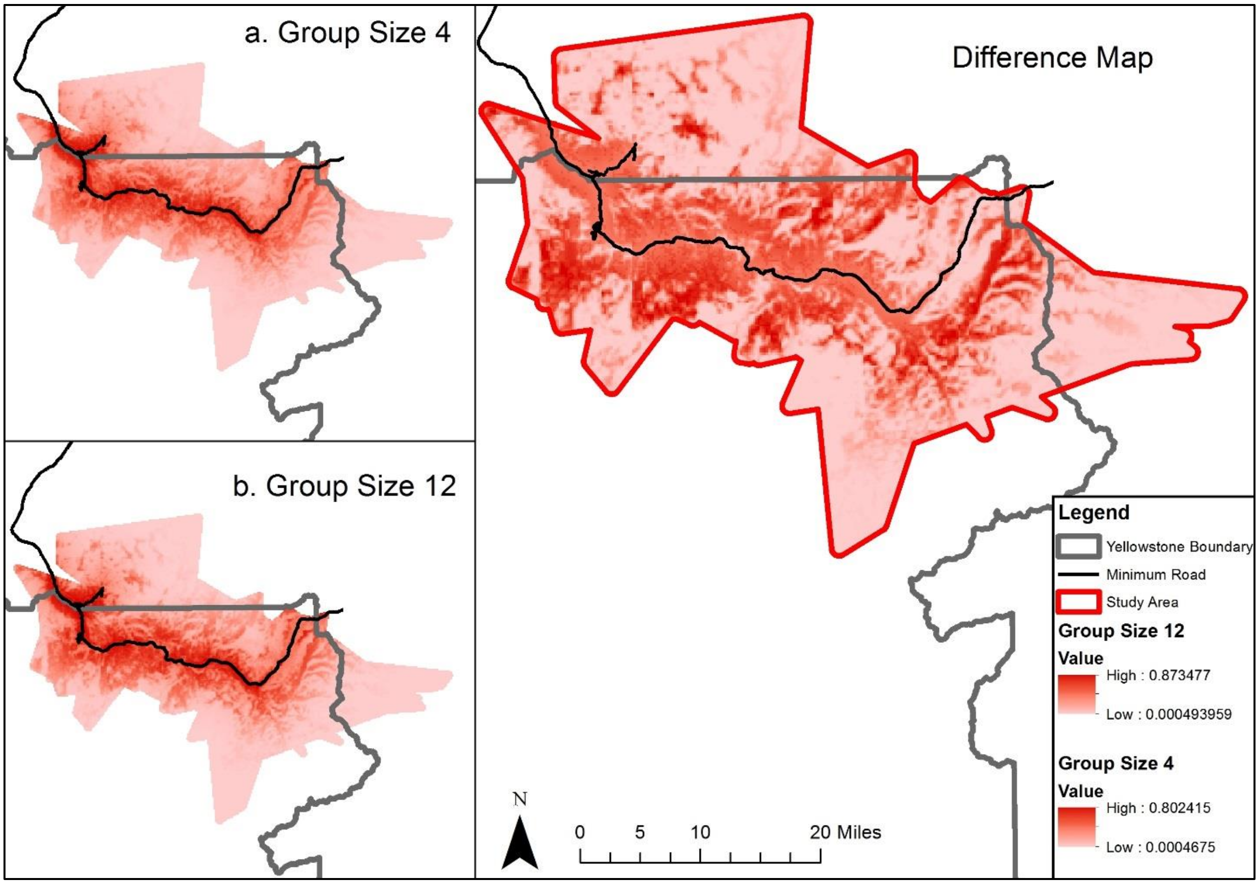

Figure 7 – Map of the probability of detecting a group of a) four gray wolves *(Canis lupus)*, b) twelve wolves, and the difference between the two groups in Yellowstone National Park, 1995-2017, in winter. These predictions came from the top used-available model. Note that areas that are close to the road had a higher probability of detection than more distant areas. Areas that are open had a higher probability of detection than closed areas. Areas that are visible had a higher rate of detection than areas that are not. The larger the group size, the higher the probability of detection. In the difference map, note that the largest differences are found in areas that are suitable for wolf sightings but at farther distances from the road.

Used-Unused Analysis - The top wolf sightability model in the used-unused analysis was similar to that in the used-available analysis, and included an interaction between distance and group size, whether the location was visible in our viewshed, and habitat openness (Table 4, Appendix 2). This model contained 53% of the AIC weight. Of the top two models, both included viewshed value, openness value, and distance to the road, and group size as covariates. All four variables held 100% of the AIC weight.

Table 4 – Top models of roadside winter gray wolf sightability in Yellowstone National Park. These models were created using a used-unused analysis. Data was collected during two annual winter study periods from 1995-2017.

Model	LL	K	Delta AICc	AICcWt	Cum.Wt
Distance * Group Size + Viewshed + Openness	-5440.86	7	0.00	0.53	0.53
Openness * Group Size + Viewshed + Distance	-5441.03	7	0.36	0.44	0.97
Viewshed + Openness + Group Size + Distance	-5441.72	6	5.73	0.03	1.00

Again, the beta coefficients from the top model indicated that the probability of detecting a wolf was higher in areas more visible from the road (Table 5, Figure 8, $\beta = 1.13$, SE = 0.055). In addition, wolves were more likely to be detected in areas with higher openness values (Table 5, Figure 9, $\beta = 0.753$, SE = 0.030). Also, group size played an important role, as larger groups have a higher detection probability (Table 5, Figure 10, $\beta = 0.091$, SE = 0.029). Finally, the probability of detecting a wolf from the road decreased by approximately 64 % for every 100 m the wolf was from the road (Table 5, Figure 8-10, $\beta = -0.64$, SE = 0.042). All p-values were less than 0.05, indicating statistical significance for covariates in our top model. The interaction indicates that the probability of detecting a group of wolves at greater distances from the road is smaller when the group size is smaller (Table 5, β = 0.118, SE = 0.042). We also created used-unused probability maps for a pack of 4 wolves, a pack of 12 wolves, and the difference between the two groups. We found that probability of detection decreased with distance, decreased in less open areas, and decreased in areas that were not visible. We also found that larger groups tend to have a higher probability of detection, especially at distance. This was identical to the used-available analysis.

Table 5 – Logistic regression estimates from the top used-unused analysis model regarding winter roadside gray wolf sightability in Yellowstone National Park. We gathered data duri ng winter study Periods between 1995 and 2017. The model is Distance * Group Size + Viewshed + Openn ess. This model contained 53% of the cumulative AIC value. Also shown are scaled SE, Z-v alue, and P-value.

	Estimate	Std. Error	Z	Pr(>|z|)
Intercept	-2.00	0.139	-14.96	< 2e-16
Distance	-0.64	0.042	-15.23	< 2e-16
Group Size	0.09	0.029	3.15	0.00166
Viewshed (0,1)	1.31	0.055	23.81	< 2e-16
Openness	0.75	0.030	25.40	< 2e-16
Distance:Group Size	0.12	0.04	2.82	0.00478

Finally, we reported the confusion matrix and classification diagnostics for the used-unused model (Table 6, Appendix 7). We found that the optimal cut point, where sensitivity = specificity was ~ 0.275. This value was used to classify any predicted location greater than 0.275

as used. In addition, any predicted location less than 0.275 was unused. Overall classification success, sensitivity and specificity for this top model were 0.72, indicating good model performance (Hosmer and Lemeshow 2000).

Table 6 – Confusion matrix of wolf used vs. unused locations from the top P(Sighting) model for wolves in Yellowstone National Park in winter. The optimal cut point, where sensitivity = specificity was ~ 0.275, which was used to classify any predicted location > 0.275 as used, and vice versa as not seen. Overall classification success, sensitivity and specificity for this top model were 0.72.

Probability of Sighting ≥ 27.5%	0	1
False	6369	847
True	2449	2154

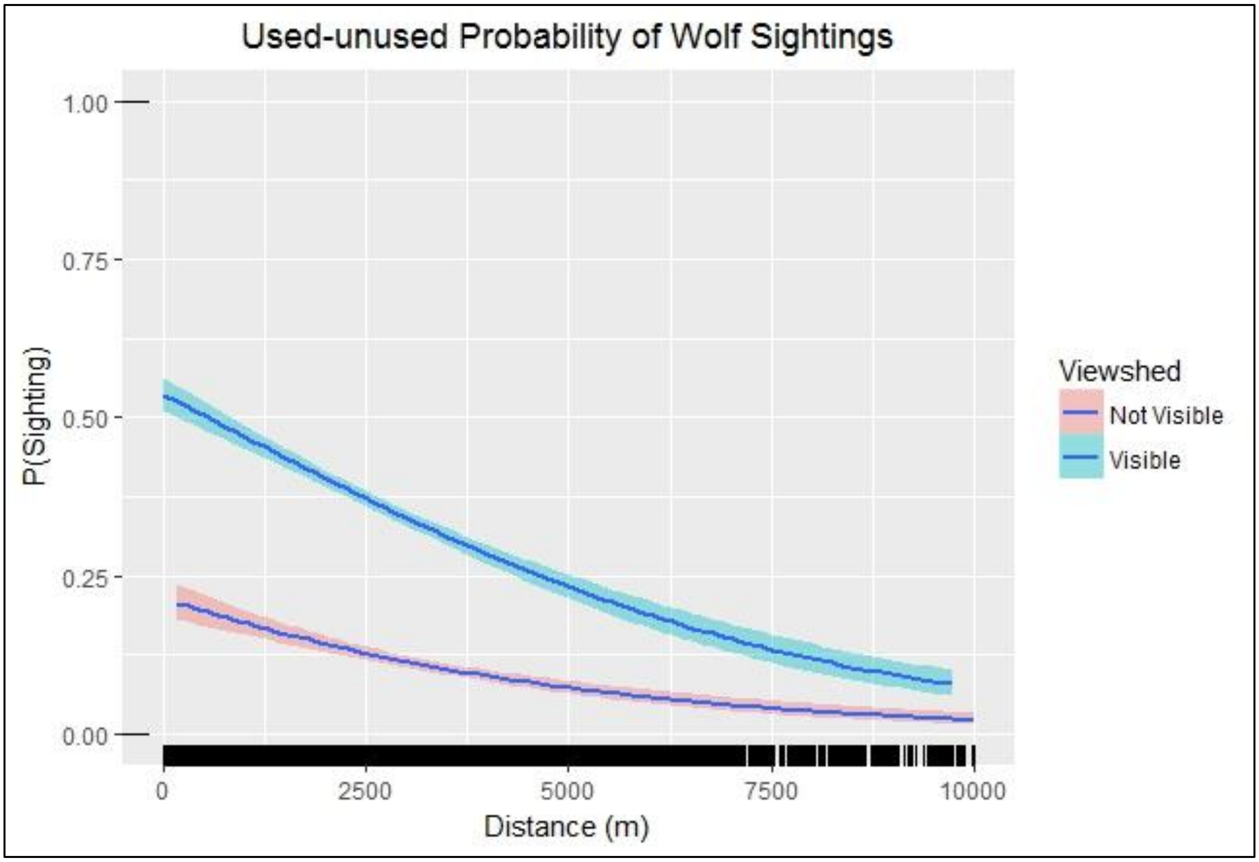

Figure 8 – Predicted probability plot of the relationship between distance to the road in meters (X) and the probability of detecting a gray wolf *(Canis lupus)* in Yellowstone National Park from 1995-2017 in areas that are visible and not visible from the road in the used-unused analysis. Overall, visible areas have a higher likelihood of wolf observations.

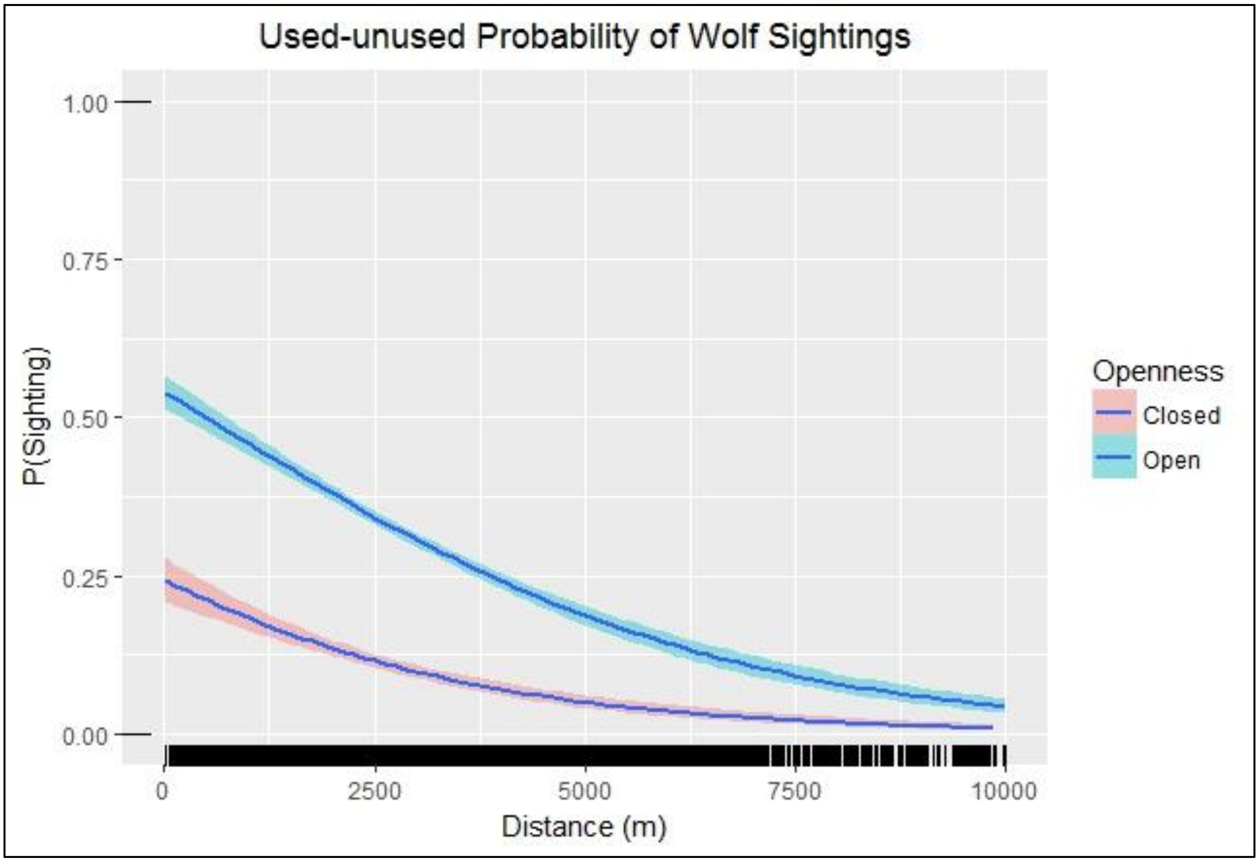

Figure 9 – Predicted probability plot of the relationship between distance to the road in meters (X) and the probability of detecting a gray wolf *(Canis lupus)* in Yellowstone National Park from 1995-2017 in areas that are open and closed in the used-unused analysis. For this graph, the continuous openness category was split down the middle to create two categories. In both categories the probability of detecting a wolf drops off dramatically as distance from the road increases. Overall, open areas have a higher likelihood of wolf observations.

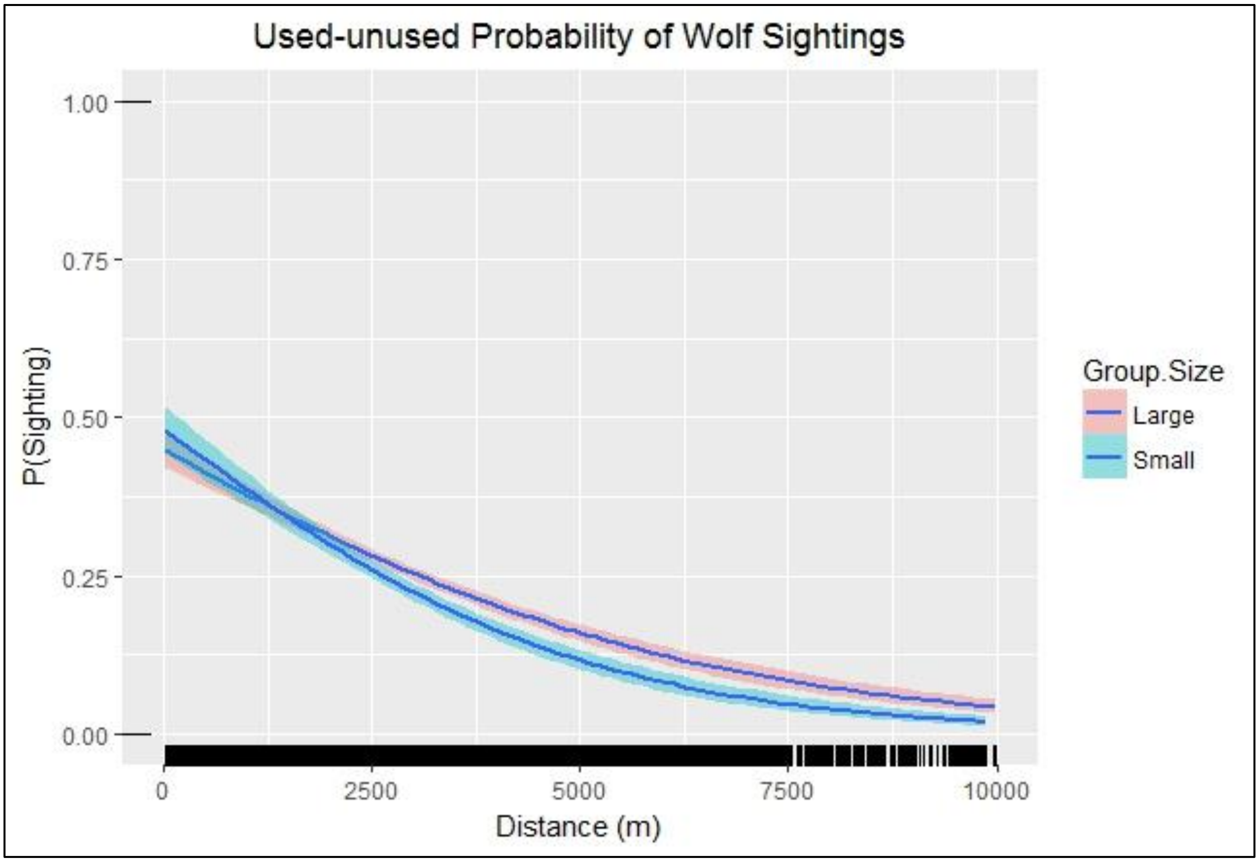

Figure 10 – Predicted probability plot of the relationship between distance to the road in meters (X) and the probability of detecting a gray wolf *(Canis lupus)* in Yellowstone National Park from 1995-2017 in large and small groups in the used-unused analysis. For this graph, groups consisting of 8 or more wolves were considered large groups, while groups consisting of 7 or less were considered small groups. In both categories the probability of detecting a wolf drops off dramatically as distance from the road increases. Overall, larger groups have a slightly higher probability of detection, especially at distance.

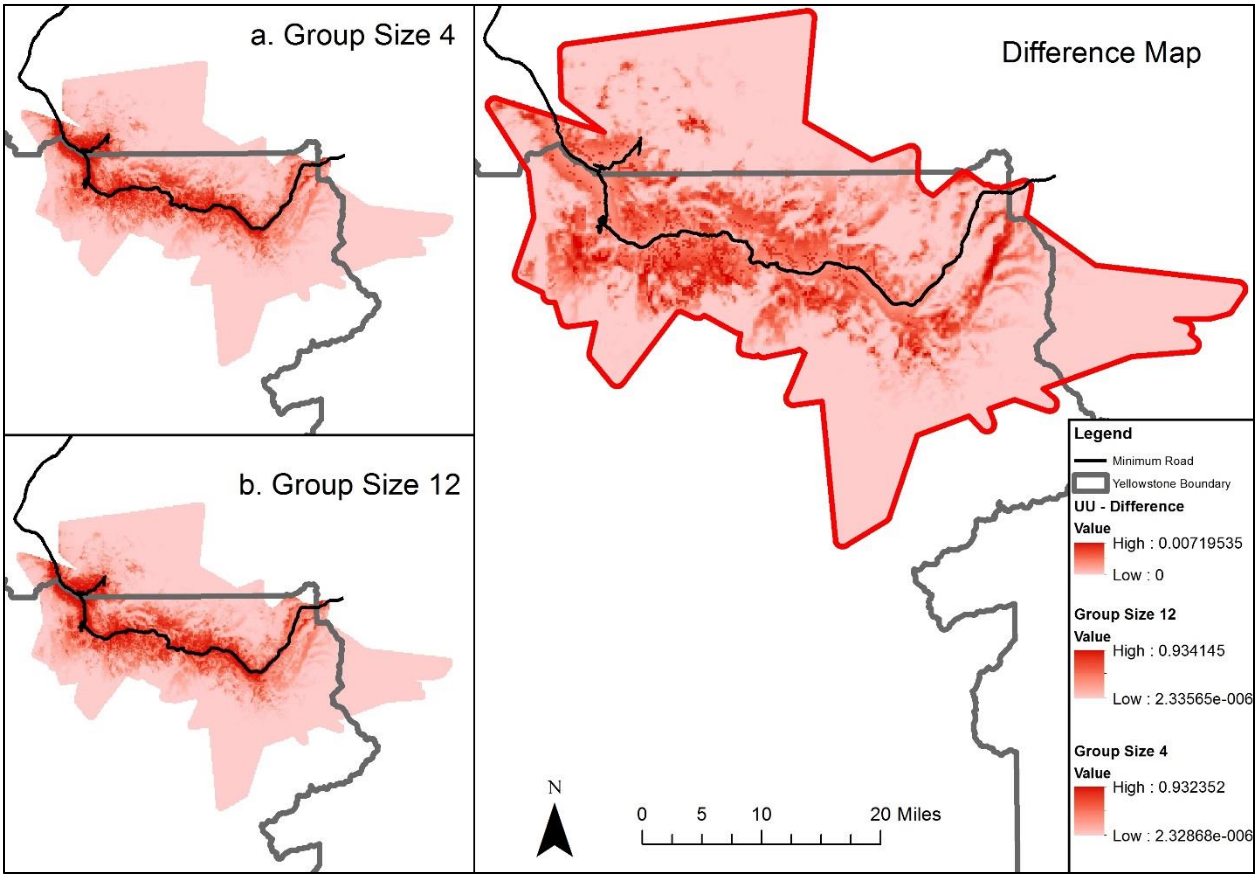

Figure 11 – Map of the probability of detecting a group of a) twelve gray wolves *(Canis lupus)*, b) four wolves, and the difference between the two groups in Yellowstone National Park, 1995-2017, in winter. These predictions came from the top used-unused model. Note that areas that are close to the road had a higher probability of detection than more distant areas. Areas that are open had a higher probability of detection than closed areas. Areas that are visible had a higher rate of detection than areas that are not. The larger the group size, the higher the probability of detection. In the difference map, note that the largest differences are found in areas that are suitable for wolf sightings but at farther distances from the road.

DISCUSSION

Our results represent one of the first times researchers have looked at factors affecting sightability for wolves in a wild setting. This could have implications for other large carnivores in other areas of high visibility. Some examples of these areas, as mentioned before, are the African Serengeti (Packer et al. 2005) and Denali National Park (Borg et al 2016) where researchers have used visual observations to estimate predator-prey dynamics, behavioral interactions, and effects of tourism on wildlife. However, unlike our study, most previous studies using carnivore observations did not explicitly account for sightability. We initially hypothesized that distance from the road, visibility from the road, group size, and carcass presence could all have impacts on wolf sightability. As expected, visibility, distance, openness, and group size all had strong effects on the probability of observing wolves, which have implications for other studies using carnivore observations. However, one factor, carcass presence, did not, according to the used-available analysis. We hypothesized that the presence of scavengers and continued presence of wolves in a given area would increase the probability of detection, but this was not the case. Our results were also very similar between our two sampling designs, used-available and used-unused, and generally showed the same covariates had similar effects on wolf sightings. These similar results between the two designs strengthen our conclusions. Our work will help park research on wolves in YNP and may also provide benefits to recreation management.

We hypothesized that the distance covariate would be of importance. We thought that as distance of the wolf to the road increased, the probability of detection would decrease. This was true according to the used-available analysis. Generally speaking, the probability of detecting a wolf declined to zero by approximately 20,000 meters (Figure 4-11). In YNP specifically, certain areas such as areas north of Hellroaring Creek near the park border had low detection probabilities (Figure 7, Figure 11). These results are similar to other sightability research. For example, the field of distance sampling rests on the principle that the probability of sightings declines with distance. Peters et al. (2014) conducted distance sampling surveys on moose in Alberta and found that probability of detection declines with distance. However, distance sampling was still more effective than stratified block designs.

We also found vegetation openness to be a significant factor affecting wolf sightability. We hypothesized that wolf detection would be higher in more open areas, and this was the case (Figure 5, Figure 9). This was true according to the used-available analysis and the used-unused analysis. In addition, we found that an interaction between openness and group size was an important factor in the top model in the used-available analysis. This same model held the second-most weight (44%) in the used-unused analysis (Table 4). This is most easily interpreted through stating that the probability of detecting large groups in areas with low openness values was higher than the probability of detecting smaller groups. This is similar to elk sightability models, in which sightability often declines with increasing tree cover (Samuel et al. 1987, Unsworth et al. 1990, Samuel et al. 1992).

Group size was also important, as we hypothesized, but only weakly, which was surprising. We found that probability of detection increased for each additional wolf in a pack (Figure 6, Figure 10). Large groups had a higher probability of detection. This was especially true at greater distances (Figure 6, Figure 7, Figure 10, Figure 11). However, the difference between large and small groups was fairly small. As mentioned above, the interaction between openness and group size indicated that larger packs had a higher probability of detection in areas with low openness values in the top model in the used-available analysis and the second model in the used-unused analysis. In addition, the top model in the used-unused analysis included an interaction between distance and group size, indicating that smaller groups are more difficult to detect at greater distances than larger groups (Table 5). Again, this is similar to group size elk sightability models (Samuel et al. 1987, Unsworth et al. 1990, Samuel et al. 1992). From a large carnivore standpoint, this method could also be incorporated with species such as African lions, which also live in groups.

The location of observations within the viewshed was also important. We found that wolves are more likely to be detected in an area that is visible from the park road and key observation points than in areas that are not visible (Figure 4, Figure 8). This makes intuitive sense, noting that detecting wolves in area that are not visible is impossible. Our findings have implications for areas that do not have roads. Such areas are more difficult to observe wildlife in, and probability of detection will likely be lower. In comparison, wolves in Denali National Park are more visible when they den near roads (Borg et al. 2016).

Finally, the only covariate that did not play significantly into our models was carcass presence. We hypothesized that the presence of scavengers such as highly visible ravens and the persistence of wolves in an area over an extended period of time would heighten the probability of the detection. However, according to our results, this was not the case. This may be due to limited of movement of wolves on a carcass, causing probability of detection to drop, counteracting the increase in detection offered by spotting scavenger activity. Overall, it was most surpsiring that the interaction term between openness and carcass detection did not have an important effect. Some of the lack of importance for the presence of a carcass may have also been due to spatial differences in the probability of detecting a carcass itself (Smith et al. 2004). We did not examine this variable in the used-unused analysis.

Minimal differences between the used-unused and used-available sampling designs also strengthen the conclusions of our study. The used-available analysis yields a relative probability because we don't know the true ratio of seen and unseen wolves. In comparison, the used-unused analysis yields a true probability (Boyce 2006, Manly et al. 2002). The more trustworthy analysis is likely the used-unused analysis because it provides a true probability. However, the used-available analysis is likely more practical for research that doesn't employ GPS collars because it is impractical to understand what occurs when animals are not in sight. The preferred alternative should be the used-unused analysis, due to its accuracy.

Transboundary management of large carnivores in national park settings is challenging, and requires interagency coordination and communication, and a scientific understanding of effects of harvest on population dynamics and behavior (Hebblewhite et al. 2007, Smither et al. 2016). One aspect of the effects of wolf harvest that is unknown is whether or not harvest affects visibility of large carnivores. Previous studies have shown changes in large carnivore behavior, such as wolves, inside and outside of national park boundaries where they protected from harvest (Thurber and Peterson 1994, Hebblewhite et al. 2008), but few have investigated effects of harvest on sightability of wolves. In one study that examined this, Borg (2016) showed that wolves in YNP and Denali National Park were less likely to be seen after harvest occurs within the pack (Borg et al. 2016). This has implications for both research and tourism. We did not explicitly test for effects of wolf harvest on sightability of wolves in our study, yet preliminary results support conclusions of Borg (2016). Wolf harvest started outside YNP in 2009, then was temporarily ceased in 2010, and the continued since 2011 (Smith et al. 2016). Like Denali, wolf harvest outside YNP's Northern Range in Montana and Wyoming may have affected behavior and abundance of wolves in Yellowstone's Northern Range (Smith et al. 2016). We did examine the effects of time on the predicted probability of observing wolves from our top used-unused model (Appendix 6), however. Examining the probabilities of observing wolves does suggest there may have been a decline in wolf sightings following 2009, but these changes might also be correlated with declining wolf elk in YNP's Northern Range. Future studies of wolf sightability in YNP should more fully examine effects of wolf harvest on wolf sightability. Also, Borg (2016) found that proximity of roads to wolf dens and the size of the wolf population were important aspects of wolf visibility. Sightability models in large carnivores should be considered in areas where they are observed on a regular basis. Some examples include lions in the Serengeti, Bengal tigers in India, or polar bears in Canada.

Some notable caveats must be noted from this study. Fortunately, these caveats do not greatly devalue the purpose of this research. There may be additional factors that impact wolf sightability. Some we considered but were not able to include consisted of snow cover, elk density, behavior, and elevation. Since our study period was during winter, snow cover was generally consistent, meaning that its exclusion likely was not significant. Elk density may also impact wolf sightability. If this covariate is important, it would likely impact the number of wolf packs in a given area, but not necessarily wolf behavior. Therefore, wolves likely would still be visible in the same areas. In fact, despite the decline of the Yellowstone elk population since the reintroduction of wolves, wolf sightings still tend to occur in similar locations. We did not consider elevation because we hypothesized that the park road was generally at low elevation, and this may cause the probability of detection to be higher at low elevations, even though this may not truly be the case. We also did not consider behavior because we would need to know the behavior for unused and available locations, which was not feasible.

Finally, locations from the used-available analysis are subject to observer error, while the locations from the used-unused analysis are probably more accurate due to being recorded by GPS collars. For the used-available analysis, the ground observations crews plotted wolf locations by hand using aerial photos or maps. This likely led to some observer error in positional accuracy that was greater than typical GPS location error which is usually under 25 meters (Hurford 2009).

It must also be noted that these observations were made by park researchers, who likely have a higher likelihood of detection than the general public. There is still likely to be a pattern between the covariates, and it is likely that the probability of sightings for visitors is at a lower baseline, but has the same overall trends due to distance, group size, visibility and openness.

CONCLUSIONS

These sightability models validate other wolf research conducted within YNP because most park studies include wolf observation. In the future, the Wolf Project seeks to use this information to estimate kill rates. In a previous study, the Wolf Project found that distance to the road was only factor that impacted detection of wolf kills (Smith et al. 2004). Our study adds that visibility from the park road, openness, and size of the wolf pack are also important factors. This will increase the precision of wolf kill detection.

Finally, this study could be used to alleviate some management issues in YNP. Since areas with a high probability of wolf sightings have been identified, management can implement wolf education in these areas, furthering human enjoyment. Also, the presence of management staff to enforce rules and regulation regarding wolves likely will lead to lessened stress on wolves and reduction in foolish human actions, which will result in safety for both wolves and humans.

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Appendix 1 – Top models of roadside winter gray wolf sightability in Yellowstone National Park. These models were created using a used-available analysis. Data was collected during two annual winter study periods from 1995-2017.

Model	LL	K	Delta AICc	AICcWt	Cum.Wt
Openness * Group Size + Viewshed + Distance	-1517.33	5	0.00	0.49	0.49
Viewshed + Distance + Openness	-1519.92	3	1.16	0.28	0.77
Distance * Group Size + Viewshed + Openness	-1518.68	5	2.70	0.13	0.90
Distance * Carcass + Viewshed + Openness	-1519.36	5	4.06	0.06	0.96
Openness * Carcass + Viewshed + Distance	-1519.91	5	5.16	0.04	1.00
Openness * Group Size + Distance	-1528.74	4	20.81	0.00	1.00
Distance + Openness	-1531.71	2	22.75	0.00	1.00
Distance * Group Size + Openness	-1530.48	4	24.29	0.00	1.00
Distance * Carcass + Openness	-1531.08	4	25.49	0.00	1.00
Openness * Carcass + Distance	-1531.71	4	26.75	0.00	1.00
Openness * Groups Size + Viewshed	-1600.81	4	164.96	0.00	1.00
Viewshed + Openness	-1603.02	2	165.36	0.00	1.00
Openness * Carcass + Viewshed	-1603.00	4	169.33	0.00	1.00
Viewshed + Distance	-1638.61	2	236.55	0.00	1.00
Distance * Group Size + Viewshed	-1637.21	4	237.74	0.00	1.00
Openness * Group Size	-1638.75	3	238.83	0.00	1.00
Distance * Carcass + Viewshed	-1637.84	4	239.01	0.00	1.00
Openness	-1641.58	1	240.49	0.00	1.00
Openness * Carcass	-1641.49	3	244.32	0.00	1.00
Distance	-1660.61	1	278.54	0.00	1.00
Distance * Group Size	-1659.28	3	279.88	0.00	1.00
Distance * Carcass	-1659.63	3	280.60	0.00	1.00
Viewshed	-1783.13	1	523.59	0.00	1.00

Appendix 2 – Top models of roadside winter gray wolf sightability in Yellowstone National Park. These models were created using a used-unused analysis. Data was collected during two annual winter study periods from 1995-2017.

Model	LL	K	Delta AICc	AICcWt	Cum.Wt
Distance * Group Size + Viewshed + Openness	-5440.86	7	0.00	0.53	0.53
Openness * Group Size + Viewshed + Distance	-5441.03	7	0.36	0.44	0.97
Viewshed + Openness + Group Size + Distance	-5441.72	6	5.73	0.03	1.00
Viewshed + Distance + Openness	-5447.53	5	9.35	0.00	1.00
Openness * Group Size + Viewshed	-5576.31	6	268.90	0.00	1.00
Viewshed + Openness + Group Size	-5580.21	5	274.69	0.00	1.00
Viewshed + Openness	-5581.74	4	275.77	0.00	1.00
Distance * Group Size + Openness	-5757.97	6	632.22	0.00	1.00
Openness * Group Size + Distance	-5758.56	6	633.41	0.00	1.00
Distance + Openness + Group Size	-5761.42	5	637.13	0.00	1.00
Distance + Openness	-5764.85	4	641.99	0.00	1.00
Distance * Group Size + Viewshed	-5820.10	6	756.48	0.00	1.00
Viewshed + Distance + Group Size	-5823.30	5	760.88	0.00	1.00
Viewshed + Distance	-5833.49	4	779.27	0.00	1.00
Viewshed + Group Size	-6013.55	4	1139.37	0.00	1.00
Viewshed	-6021.47	3	1153.22	0.00	1.00
Openness * Group Size	-6030.62	5	1175.53	0.00	1.00
Openness + Group Size	-6033.26	4	1178.80	0.00	1.00
Openness	-6034.51	3	1179.30	0.00	1.00
Distance * Group Size	-6193.90	5	1502.08	0.00	1.00
Distance + Group Size	-6197.46	4	1507.19	0.00	1.00
Group Size	-6559.62	3	2229.52	0.00	1.00
Distance	-6209.59	3	1529.46	0.00	1.00

11/07/11

Data entered into database: (initials) DP
Data in database double checked:

Winter Study – Daily Activity Summary

PAGE 1

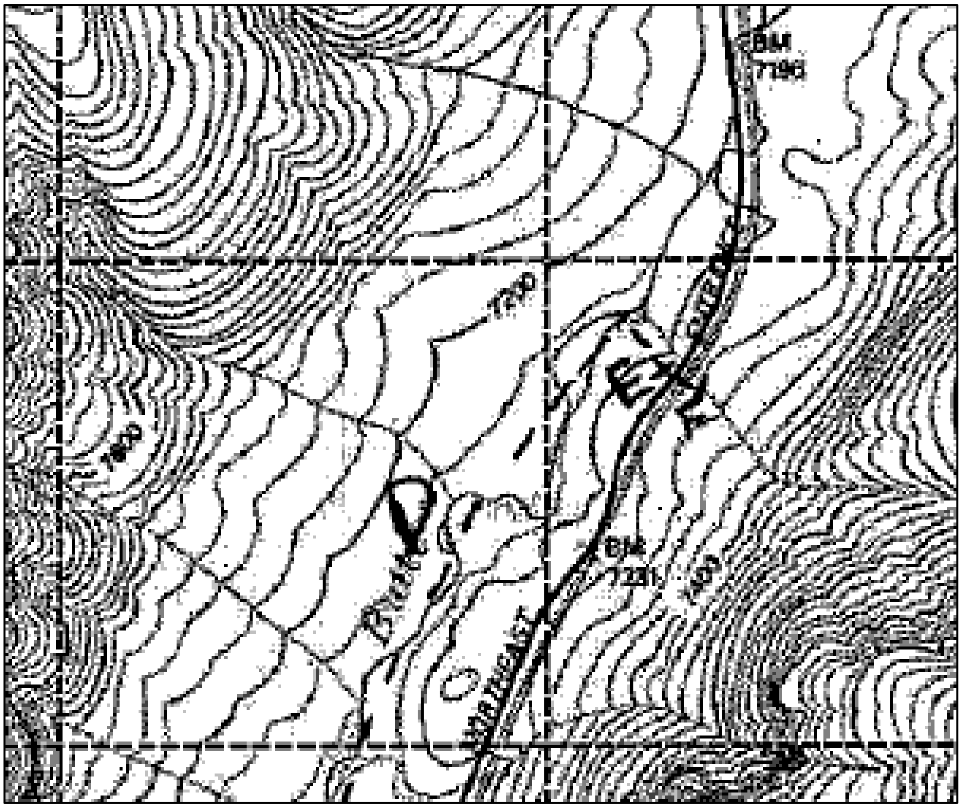
path: O:\ADMIN\Data Forms\Winter Study\Daily Activity Summary.doc

(EXAMPLE DATA ON BACK)

Pack: Lamar Canyon **Date:** 3/2 **Year:** 2012 **Obs:** H. Martin, C. Anton, J. Tasch

Point/ Route	Time Start	Time End	Activity Type [1]	Sleep/Rest (minutes)	Travel (minutes)	Hunt (minutes)	Feed (minutes)	OOS (minutes)	Other [2] (minutes)
A	8:03	8:03	MILL						1.
B	8:04	8:56	OOS					53	
C	857	858	TRAVEL		2				
D	859	1139	OOS					161	
E	1140	1145	Travel		6				
F	1146	1807	OOS					382	
G									
H									
I									

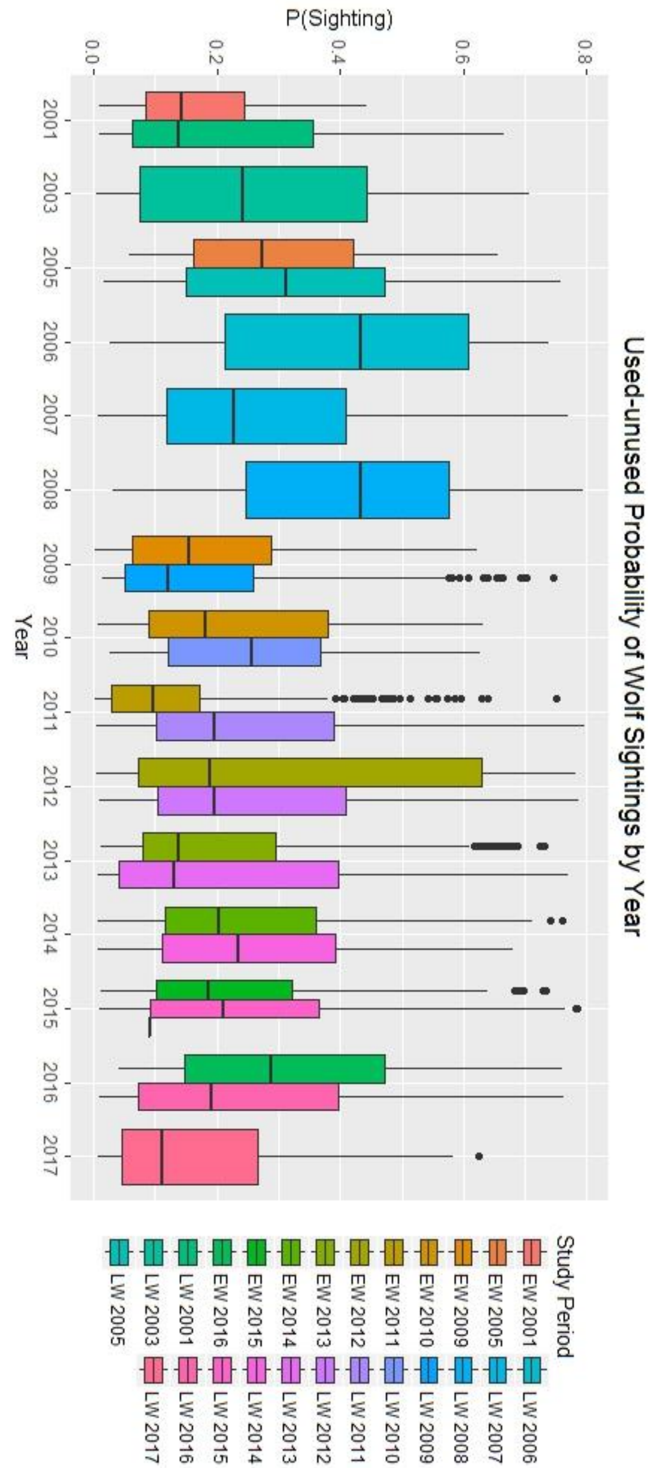
Appendix 3 – Daily activity summaries of the Lamar Canyon wolf pack in late winter 2012 in Yellowstone National Park. Points D-F are mapped in appendix 4. These forms were used to populate the database for the used-unused analysis.



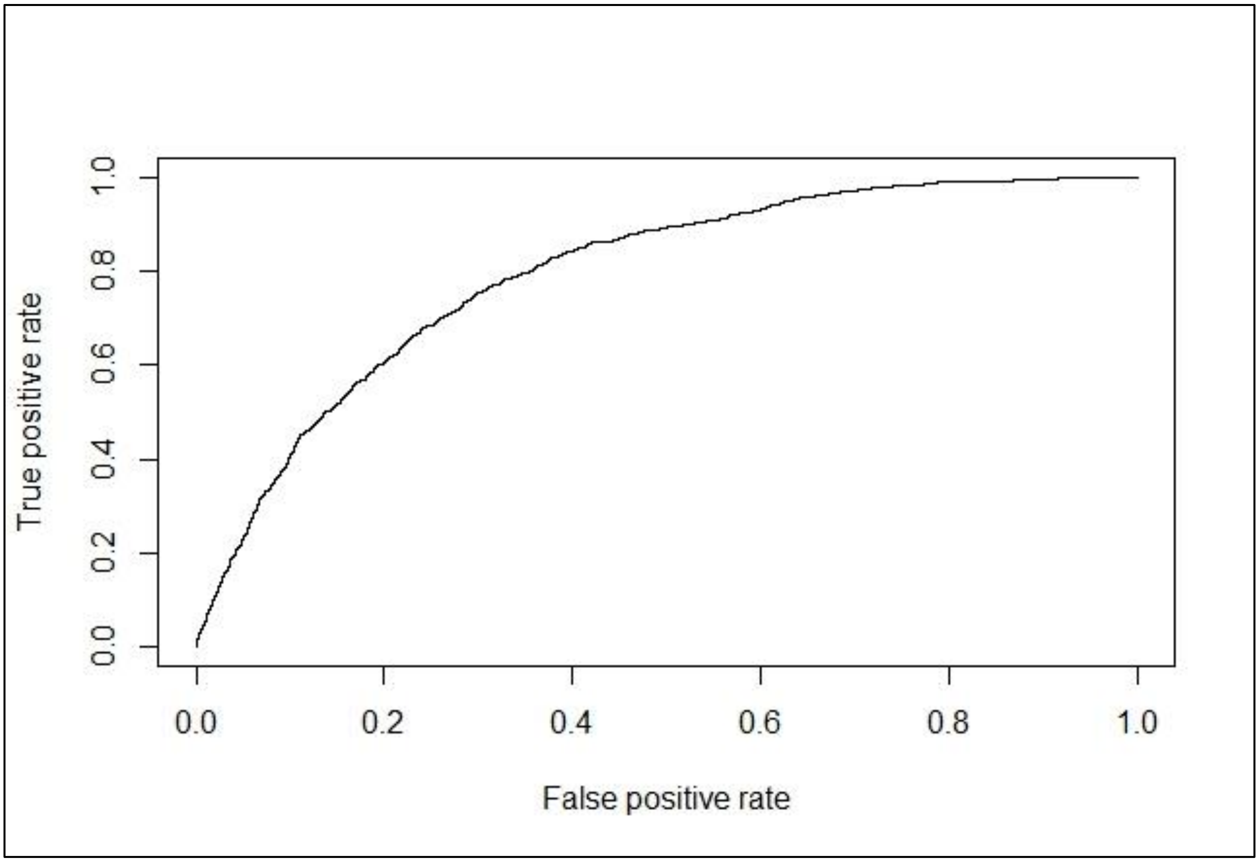
Appendix 4 – Mapped locations from daily activity summaries of the Lamar Canyon wolf pack in late winter 2012 in Yellowstone National Park. Points D-F represent the same points from Appendix 2. These forms were used to populate the database for the used-unused analysis.

mtn.date	mtn.time	easting	northing	observable	in.sight	group.size.locs.dbase	group.size	on.kill.locs.dbase	on.kill
3/1/2001	13:00:53	559249	4975320	YES	YES	24	24	Yes	YES
3/1/2001	15:01:07	559425	4974779	YES	YES	24	24	Yes	YES
3/1/2001	17:00:41	559525	4974757	YES	YES	24	24	Yes	YES
3/1/2001	18:01:06	559854	4974763	YES	NO	24	24	Yes	YES
3/2/2001	15:00:37	558923	4974527	YES	YES		19		NO
3/2/2001	17:00:15	558912	4974524	YES	YES		19		YES
3/2/2001	18:00:37	558935	4974832	YES	YES		19		YES
3/3/2001	13:00:38	559740	4974325	YES	YES	11	11	Yes	YES
3/3/2001	15:00:37	559738	4974334	YES	YES	11	11	Yes	YES
3/3/2001	17:00:49	559667	4974193	YES	YES	11	11	Yes	YES
3/3/2001	18:00:38	559579	4974206	YES	YES	11	11	Yes	YES

Appendix 5 – Example data frame from the Lamar Canyon wolf pack in late winter 2012 in Yellowstone National Park. We populated the columns “in.sight”, “group.size”, and “on.kill” manually.



Appendix 6 – Predicted probability of wolf detection by year and study period according to the used-unused analysis in Yellowstone National Park. Wolf harvest began in neighboring states in 2009.



Appendix 7 – Receiver operating characteristic (ROC) curve for the used-unused model of probability of wolf sightings in Yellowstone National Park in winter. The optimal cut point, where sensitivity = specificity was ~ 0.275, which was used to classify any predicted location > 0.275 as used, and vice versa as not seen. Overall classification success, sensitivity and specificity for this top model were 0.72.